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AGRICULTURAL MEMORANDUM No 977

A Simple Model of Part of the Life Cycle of Brachycaudus Helichrysi

by C.J. HUME

1. Introduction

During the past 15 years or so a network of insect suction traps has been established over much of the U.K. Now comprised of about 23 traps the network provides information on the spatial and temporal variations of the flying population of a range of insect species - in particular aphids. Data from the traps (and much of the analysis of individual trap catches) is collated by the Rothamsted Insect Survey (RIS) - Taylor et al (1982).

A considerable quantity of data has accumulated and it seems now opportune to examine the data from an agrometeorological point of view. To this end an attempt has been made to relate the catches of a single species (Brachycaudus helichrysi) at a single site (Long Ashton) to weather and hence to estimate the feasibility of devising a forecasting scheme for some aspects of the life cycle. A crude modelling approach has been used.

2. Brachycaudus helichrysi

The aphid (also known as the leaf curling plum aphid) is a pest of damsons and plums (Prunus domestica) which are amongst its winter hosts - other hosts include sloe (Prunus spinosa) and hawthorn (Crataegus). In addition to causing direct feeding damage the aphid is a vector of plum pox (Sharka disease - a virus disease) and a number of non persistent potato viruses. In late spring/ early summer the alate (winged) form of the aphid is produced and migration to the summer hosts occurs. The summer hosts are various clovers and compositae (eg daisies, dandelions, hawkweeds). It is during this active period that (newly emerged) potato plants are at risk (Bell, 1983)

Further details of the aphid, and its control, are contained in MAFF Leaflets 611 (1978) and 641 (1979), much of the information in which is derived from Bennett (1955) who studied the insect by rearing it on twigs of damson stuck in damp sand and placed out of doors in wire netting cages.

Figure 1a shows a rough outline of the life history of the aphid, based upon the work of the last author. The only other significant sources of data on the aphid in the UK are (a) Wyatt and Brown (1977) who describe laboratory studies and (b) Bell (1983) who reports results from N. Ireland. Figure 1b shows the weekly trap catches at Long Ashton in a typical year (1979)

3. A simple model of the life cycle

3.1 Estimation of basic parameters

Although Bennett (1955) describes the life cycle, quantitative detail is lacking. The main source of such data is Wyatt and Brown (1977) who

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describe the effects of light intensity, daylength and temperature on the aphid. Some of their results are reproduced in Table 1.

3.1.1 Estimation of threshold temperature (Tt)

Figure 2 shows the rate of development (the reciprocal of pre-productive time, table 1) from egg hatch to production of first young, plotted at the two temperatures, for various conditions of light intensity and daylength. The value of Tt (when development rate is zero) is thought to be about 4°C; inserting a bogus data point at (4,0) and fitting a straight line yields a value of 3.2°C for Tt. This dubious procedure gives a reasonable value for Tt and ensures that the (assumed linear) dependence of development rate with temperature is in accord with the very limited amount of experimental data. In the model a value of 3.2°C is therefore used and is regarded as independent of light intensity and daylength. The effect of other values of Tt is discussed later.

The rate of development (DR) derived above is given by

$DR = 0.0057(T-Tt)\ day^{-1}$ $(T > Tt)$ and

$DR = 0$ $(T \leq Tt)$

where T is temperature (°C).

The development times at 18°C/24°C are respectively 11.8 days and 8.4 days - corresponding to 175 degree-days above threshold.

3.1.2 Estimation of longevity

Longevity, expressed in degree days above threshold (3.2°C) for all of the conditions used by Wyatt and Brown (1977) is shown in table 2. The low values at low light levels have been disregarded; the mean of the remaining 4 values at 18°C is 734 degree days and of the remaining 5 values at 24°C is 796 degree days. The difference is not significant and the overall mean value of 795 degree days has been adopted.

3.1.3 Estimation of number of young

Table 1 shows low numbers of progeny at low light levels. These low values have been disregarded; the mean of the remaining 4 values at 18°C is 35 (sd 14) and of the remaining 5 values at 24°C is 41 (sd 14). The difference is not significant and the overall mean value of 38.2 has been used.

3.1.4 Estimation of reproductive time

The time during which the aphid is considered capable of reproduction is: (longevity - development time) ie 795-175 degree days ie 620 degree days (above Tt).

3.1.5 Estimation of reproductive rate

Reproduction is assumed to take place at a continuous uniform rate given by number of progeny/reproductive time ie 38.2/620 ie 0.0616 nymphs/adult/degree day.

3.1.6 Estimation of egg mortality

There are no experimental data on the mortality of eggs of this species. Mortality is ignored but use of mortality data for another species is discussed later.

3.1.7 Estimation of rate of egg hatch

Bennett (1955) counted the number of eggs (on isolated twigs of damson) during the hatching seasons of 1952 and 1953. The number of unhatched eggs (N) decline roughly exponentially with time:

$$N = No \exp(-Kt)$$

where t = time (days) from start of counting
No = number of unhatched eggs at start of counting
K = a constant (day^{-1})

The constant K is temperature dependent; using data on dry bulb screen temperature from the Long Ashton agromet station suggests a relationship:

$$K = 0.011 + 0.007T \ (day^{-1})$$

3.1.8 Estimation of diapause of the eggs

No accurate data on diapause are available. Bennett (1955) points out that unlike those of most fruit aphids, the eggs of this species hatch soon after being laid; the shortest time he noted was 26 days. For the purposes of the model the diapause is regarded as a variable. It is normally set to zero; the result of varying diapause is discussed later.

3.1.9 Estimation of Maturing time of Nymphal Fundatrices

Bennett (1955) states that nymphal fundatrices become mature in 6 to 8 weeks. A value of 7 weeks is used in the model; variation of this factor is discussed later.

3.2 The model

Using the estimates described in the previous section a computer program to simulate the life cycle of the aphid has been developed.

The program is based upon a large number of arrays containing (as either input data or as values calculated in the program) daily values of accumulated temperatures, the number of eggs laid, the number of nymphal fundatrices, the number of mature fundatrices and finally the numbers of nymph and mature aphids in generations following.

Egg laying is assumed to coincide with the arrival of males (typically in Sept/Oct) as indicated by the trap catches. The daily rate of egg laying is taken to be equal to the average daily number of males caught during each week. Since only small numbers of males are caught (say 2 per week) the daily egg laying rate is fractional ($\sim 0.28\ day^{-1}$).

Egg mortality and diapause are normally set to zero. Eggs are hatched at a temperature dependent rate as described previously; the temperature is the mean daily air temperature (Tmax + Tmin/2).

After hatch, the nymphal fundatrices (F - stage nymphs) do not start reproducing until a maturing time, normally set to 49 days (of real time rather than physiological time as expressed by degree days) has elapsed. At the end of the maturing time, the (now adult) aphids each reproduce at a daily rate of 0.0616 nymphs per deg day above Tt for the next 620 degree days (above Tt) after which they make no further contribution and are disregarded.

The nymphs produced during this stage (denoted as 'F+1 nymphs') are accumulated in an array and aged (physiological time) until, upon reaching an age of 175 deg days (above Tt) they become mature (and denoted 'F+1 matures') and are transferred to another array. These aphids reproduce at a rate of 0.0616 nymphs/adult/deg day for the next 620 deg days, after which they are no longer considered; the products of their reproduction (referred to as 'F+2 nymphs') are stored in another array. This process is repeated for a large number of generations.

The output of the model is in tabular form; giving the daily and weekly numbers of eggs and of nymphs and adults of each generation. Figure 3 shows the results plotted for 1978/79.

4. Results

The output of the model represents aphid populations growing in situ unlimited by factors such as parasites, predators and food supply; it is unrepresentative of the real situation.

With no information on these limiting factors it has been necessary to resort to statistics. Relationships between some aspects of the model output and the 'real' situation (in terms of trap catches) have been derived statistically.

4.1 Timing of the first migration

The timing of the summer migration can be characterised by the date (in terms of day number) of catch of the first aphid (often known as the date of first flight; it will be denoted DOFF); this is a rather variable feature and spans a range of about 5 weeks. A more stable parameter is the date by which a total of 10 aphids have been trapped (denoted DOT). Table 3a shows dates observed at Long Ashton.

Bennett (1955) suggests that winged aphids generally appear in the (F+4) generation. Figure 4a shows the relation between the observed value of DOFF at Long Ashton and the day number (denoted DATT) at which the model population of (F+4) mature aphids exceeds a (arbitrary) threshold of 10^4 aphids.

The best fit linear relation is

$$\hat{DOFF} = 23.73 + 0.73 * DATT \qquad (1)$$

The quality of the fit is insensitive to the value of threshold, at least for thresholds ranging from 5 10^3 to 10^7.

A similar procedure has been adopted to obtain an equation for DOT (fig 4b):

$$DOT = 96.61 + 0.32 * DATT \quad (2)$$

Again, the quality of fit is insensitive to the threshold value.

Table 3a shows the observed and calculated values of DOFF and DOT for each of the years used in deriving the best fit equations. Table 3b compares the standard deviations of observed values of DOFF, DOT with the r.m.s. differences between observed and calculated values. The calculated values have a smaller scatter than that which would be obtained by taking the averages of the observed values of DOFF, DOT.

4.2 Size of the first migration

The size of the summer migration (henceforth denoted SSM) can be characterised by the total catch during weeks 20 to 30 inclusive (fig 1b)

Since the model populations are unrealistic it has been necessary to examine the observed data for a parameter related to the size of the summer migration (SSM). There is a (very) rough inverse relationship with DOT (fig 5).

A 'reasonable' fit is the equation

$$SSM = 1538898*EXP(-0.0529*DOT) \quad (3)$$

This equation is a slightly better fit than the best linear relationship but still has a rather poor correlation coefficient. (SSM is a very variable quantity with a standard deviation of about 60% of the mean).

Table 4a shows observed and calculated values of SSM for each of the years used in deriving equation (3). Up to about June the value of DOT would be unknown and would be calculated (as described in the previous section) and inserted in (3) to provide a forecast of SSM. Later in the season DOT would be known by observation and this value used to operate an updated forecast. Thus table 4a shows two calculated values of SSM - one using an estimated value of DOT and the other using an actual value of DOT.

Table 4b compares the r.m.s. errors of the two calculated values of SSM with the observed standard deviation of SSM. The population estimate made early in the season has a slightly greater variability than the actual population but later in the season a rather better estimate (showing less variability) is possible.

4.3 Use of the model

The model has been used to forecast the timing and size of the summer migration for the years not involved in the derivation of equations (1) to (3) (ie 1974, 1981 (SSM only), 1982). Table 5 compares observed and calculated values.

The forecasts of DOT seem reasonable (errors of one and four days) but those of DOFF are poor (17 and 9 days) although this latter is observed to be very variable.

The forecasts of SSM (using either calculated or observed values of DOT) are extremely poor, involving gross over-estimation of populations or under-estimation by a factor of 2. In 1982 the results (using a calculated value of DOT) were positively misleading in suggesting a larger migration than the previous year when in fact there was a reduction by a factor of two.

5. Sensitivity tests

As described previously quantitative detail of many of the required factors has been found to be lacking; the response of the model to variation of some of the factors has been examined. The model has been used to simulate populations in 1979 using a variety of values of threshold temperature, egg mortality, egg diapause, time of egg laying and maturing time of nymphal fundatrices; the effects on DOT are considered here.

5.1 Variation of threshold temperature

Variation of this factor also influences longevity and reproduction time (both measured in physiological time) and hence reproduction rate. Figure 6a shows the value of DOT for a variety of threshold temperatures. Up to about 8°C DOT is almost linearly related to Tt; the rate of change of DOT is about 4 days per deg C. At warmer thresholds the development of the population over winter and spring becomes increasingly retarded resulting in an increasing delay in DOT.

5.2 Variation of egg mortality

There are no data on egg mortality for Brachycaudus helichrysi. To obtain an estimate of likely effects mortality data for another species - Rhopalosiphum padi (the Bird cherry-oat aphid) - have been utilised (Leather, 1980, 1981). In this work mortality was attributed to predation by arthropods (and to a small extent by birds) and to rain (both directly by dislodgement and indirectly by facilitating fungal growth). This author presents data on the number of eggs (laid on Prunus padus) surviving as a function of time from about mid-November onwards. Up to about mid-February the fraction surviving can be fitted by:

$$\text{Fraction surviving} = 1 - bt$$

where b is a constant (the loss per day) and t is time in days. Values for b of 0.0033 and 0.0056 were obtained from the data of Leather (1980, 1981). By mid-February the population of (F+1) mature aphids is increasing and the contribution from further egg hatch is unlikely to significantly change the timing of the (F+4) generation.

The effect of varying b between zero and 0.02 has been examined and found to change DOT by less than 1 day - a negligible effect.

5.3 Variation of egg diapause

Diapause deviation has been varied from zero to 80 days with the effect shown in fig 6b. No attempt has been made to introduce any temperature dependence of diapause. In general DOT is rather insensitive to diapause.

At low diapause values (up to about 40 days) significant population development occurs before the onset of winter and DOT is relatively sensitive to diapause (at a rate of roughly 0.25 days per day of diapause). At greater diapause values (up to about 90 days) the early stages of population growth are delayed into winter where physiological time passes slowly and sensitivity is reduced. For even longer diapauses, population growth is displaced towards warmer temperatures and the sensitivity of DOT returns. Overall, the sensitivity is low.

5.4 Variation in time of egg laying

As mentioned earlier the daily rate of egg laying is taken as equal to the average daily rate of catch of males - this was necessitated by the trap catch data being presented as weekly totals. The dependence of forecast values of DOT upon variations in egg laying has been estimated by varying the start of the egg laying 'season' used to forecast the 1979 populations. The result is shown in fig 6c; the rate of change of forecast value of DOT is about 0.3 days per day of the start of the egg laying season.

5.5 Variation of maturing time of nymphal fundatrices

Figure 6d shows the result on DOT of variations of this factor. As for diapause, maturing time is expressed in clock time rather than physiological time. As in the case of diapause, the sensitivity decreases with increasing maturing time, again because of the shift towards winter of the period of population development. Up to a maturing time of about 60 days the rate of change of DOT is around 0.3 days per day of diapause.

5.6 Summary

The forecast value of DOT is most sensitive to Tt but dependence on the time at which eggs are laid and upon the maturing time of nymphal fundatrices are also significant.

6. Discussion

6.1 Construction of the model

The previous section showed the output of the model to be sensitive to a number of factors. The sensitivity is roughly linear over the probable likely ranges of values of the factors.

Although greatest sensitivity is to Tt the measurement of a more accurate value (if indeed a single value is appropriate) than the rather artificially derived 3.2°C would be of limited practical value. In the field the relation between screen air temperature (the only operationally available measure of temperature) and the temperature experienced by an aphid in its habitat is complex and open to sufficient uncertainty as to make a precise value of Tt of little practical use.

Both egg diapause and nymphal fundatrix maturing time have been taken as independent of temperature which is almost certainly incorrect. The sensitivity to these factors is significant and further data are necessary.

Egg mortality seems not to be an important factor but some evidence that the mortality causes and rates assumed in section 5.2 are reasonable is required.

Considering egg laying, daily catches are available from the RIS but more detail on the mating (mate seeking may be weather sensitive) and egg laying behaviour are required.

The model is flexible in that further biological knowledge can be inserted and the model 're-calibrated' via the regression equations (1), (2) and (3).

Turning now to more general aspects, the model can be criticised on a number of counts. It is based on a single study (Bennett, 1955) of the life cycle, observed under artificial conditions - twigs in damp sand - which may affect the cycle. Also, no attempt has been made to model the wintertime intermediate stage (which may occur when autumn is mild) indicated by that author (fig 1a). It is also possible that in the 30 years since the study the cycle has significantly changed. A similar question may arise concerning the behaviour in different parts of the UK.

The life cycle has presumably become adapted to ensure survival in extreme conditions. Details of the survivability are unknown. The egg diapause is unusually short (Bennett (1955) - he noted 26 days as the shortest period) which suggests a high survival rate but there may be compensation by high mortality in the overwintering fundatrix and (F+1) stages.

So far the only influence of weather that has been considered has been mean air (screen) temperature. An effort has been made to examine the population fluctuations with respect to other elements - maximum and minimum temperatures, grass minimum temperature, daily rainfall and daily sunshine - at Long Ashton. The approach adopted has been to correlate the size of the summer migration with average values of these elements. Averages have been taken over varying periods of time starting at various times of the year. An example is shown in fig 7. For all of the elements concerned and for averaging periods of 5 days to 60 days no clearly significant correlations were found.

Obviously a more discriminating approach to the effects of weather on the aphid is needed and there is a requirement for entomological advice on some possible weather based mechanisms of mortality.

6.2 Results of the model

6.2.1 Timing

Comparisons of forecast and actual values are limited by lack of independent data. However, in the two years when comparison is possible (table 5) the forecasts of DOT seem reasonable. The much poorer forecasts of DOFF are perhaps not too important since this is a naturally very variable quantity and is unlikely to be of great use in an operational scheme for predicting summer migration.

6.2.2 Size

The forecasts of SSM - the size of the summer migration - are very poor although, again, comparative data are limited. The poor performance is a reflection of the considerable scatter in the relationship between migration size and the adopted predictor - DOT (fig 5)

Clearly a greater understanding of the year-to-year population fluctuations is required. As described in section 6.1 no clear relationship between SSM and a variety of aspects of the past weather were found. The relationship with contemporaneous weather has therefore been examined and some preliminary results outlined here.

The flight of alate aphids is generally thought to be influenced by prevailing weather conditions - flying is inhibited when (poorly known) weather criteria fall below certain (also poorly known) thresholds. Evidence for such thresholds for B. Helichrysi has been sought by studying the relation between SSM (or, more strictly, the trap catches reflecting the migration) and the duration for which a number of weather elements (windspeed, dry bulb temperature, total cloud cover) have satisfied various criteria.

The nearest source of hourly data is that from Filton (the station closed in 1979). Figure 8a shows SSM measured at Long Ashton (for the years 1970-73, 1975-79) plotted against the total number of hours (in May, June and July (weeks 18-30 inclusive)) when windspeed (at 10m) was less than or equal to a threshold of 10 kt. Only daylight hours (taken to be roughly 0400 to 2100Z) were considered. The correlation coefficient (r) is significant at around the 2% level. Correlation coefficients for a variety of thresholds are shown in fig 9a; there is a maximum around 10-15 kts. Similar analyses have been performed for (i) number of hours with total cloud cover less than or equal to a number of thresholds and (ii) number of hours with dry bulb air temperature greater than or equal to a number of thresholds. Figures 9b, c show the respective variations of r; of the three weather elements considered, wind has the greatest effect.

The next nearest hourly reporting station is Rhoose (although Lyneham is at a similar distance); using weather data from this site and trap data for 1970-73 and 1975-80 gives consistently lower correlations - also shown in figs 9a, b and c.

The mechanism by which wind influences trap catches is not clear. As indicated earlier one possibility is inhibition of aphid flight in high winds; another factor may be dependence of trap collection efficiency upon wind speed. A related factor may be that greater windspeeds 'import' aphids from further afield and present them for collection by the trap.

Whatever the mechanisms are involved, the role of contemporaneous weather in the interpretation of trap catches seems to be a relevant factor in improving the model.

A further essential factor affecting populations is the presence of parasites and predators - factors not considered in the model. Entomological advice is essential here.

7. Summary

A simplistic, temperature based model of part of the life cycle of the leaf curling plum aphid has been described.

Forecasts of the timing of the summer migration are reasonable but those of the size of the migration are very poor.

Improvements to the model depend upon more information concerning the life cycle (especially mating and egg laying behaviour), quantitative data on egg diapause, egg mortality, maturing time of nymphal fundatrices and perhaps most importantly the effects of parasites and predators. A further feature requiring study is the role of contemporaneous weather in the interpretation of the trap catches reflecting the size of the summer migration. Finally, entomological advice on parasites and predators is required.

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Table 1

Developmental and reproductive data for Brachycaudus Helichrysi on chrysanthemum leaves in a laboratory environment (from Wyatt and Brown (1977)).

Light Intensity (lux) / Daylength (hrs)	800		4000		8000	
	8	16	8	16	8	16
Temperature = 18°C						
Preproductive time n (days)	12.6	12.5	10.5	11.7	10.0	12.4
Mean generation time T (days)	14.9	13.8	17.7	17.3	15.3	17.2
Mean longevity (days)	12.0	12.3	56.3	62.6	42.9	52.5
Mean progeny	3.3	2.9	46.0	32.8	44.4	15.8
Temperature = 24°C						
Preproductive time n (days)	9.0	8.5	8.3	8.5	9.5	7.8
Mean generation time T (days)	11.6	12.4	13.0	12.9	14.9	12.1
Mean longevity (days)	8.8	40.0	44.3	28.3	42.3	36.5
Mean progeny	0.6	63.0	42.1	23.7	41.8	34.0

Table 2

Longevity in degree days above 3.2°C (derived from the data in table 1)

Light Intensity (lux) / Daylength (hrs)	800		4000		8000	
	8	16	8	16	8	16
Temperature = 18°C						
Longevity (deg days)	177.6	236.8	833.2	926.5	634.9	777.0
Temperature = 24°C						
Longevity (deg days)	183.0	832.0	921.4	586.6	879.8	759.2

Table 3a

YEAR	OBSERVED		CALCULATED	
	Day No. of first Catch (DOFF)	Day No. of tenth Catch (DOT)	Day No. of first Catch (DOFF)	Day No. of tenth Catch (DOT)
1970	(133)	(147)	-	-
71	121	134	123.2	140.5
72	139	153	126.2	141.8
73	115	140	123.7	140.7
74	(136)	(138)	-	-
75	115	138	113.0	136.0
76	127	141	140.5	148.1
77	145	148	138.0	147.0
78	129	145	128.8	143.0
79	147	154	141.5	148.6
1980	133	136	125.7	141.6
81	113	139	123.7	140.7
MEAN	129.1	142.4	128.4	142.8
STD DEVN	12.1	7.0	9.0	4.0
N	10	10	10	10

(Values in brackets not used in derivation of regression equations)

Table 3b

	DOFF	DOT
Observed STD DEVN (days)	12.1	7.0
RMS Difference of (Observed-Calculated) (days)	8.5	5.7

Table 4a

YEAR	OBSERVED		CALCULATED		
	Total aphid catch in summer migration (SSM)	DOT	DOT	Total aphid catch in summer migration (SSM)	
				Using Calculated DOT	Using Observed DOT
1970	985	147	-	-	645.7
71	2007	134	140.5	910.6	1284.3
72	301	153	141.8	850.1	470.1
73	522	140	140.7	901.0	935.0
74	(2453)	(138)	-	-	
75	744	138	136.0	1155.4	1039.4
76	948	141	148.1	609.2	886.9
77	300	148	147.0	645.7	612.4
78	1588	145	143.0	797.8	717.7
79	690	154	148.6	593.3	445.8
1980	1050	136	141.6	859.1	1155.4
81	(289)	(139)	-	-	-
MEAN	913.5			813.6	819.3
STD DEVN	543.6			178.9	286.8
N	10			9	10

(Values in brackets not used in derivation of regression equations)

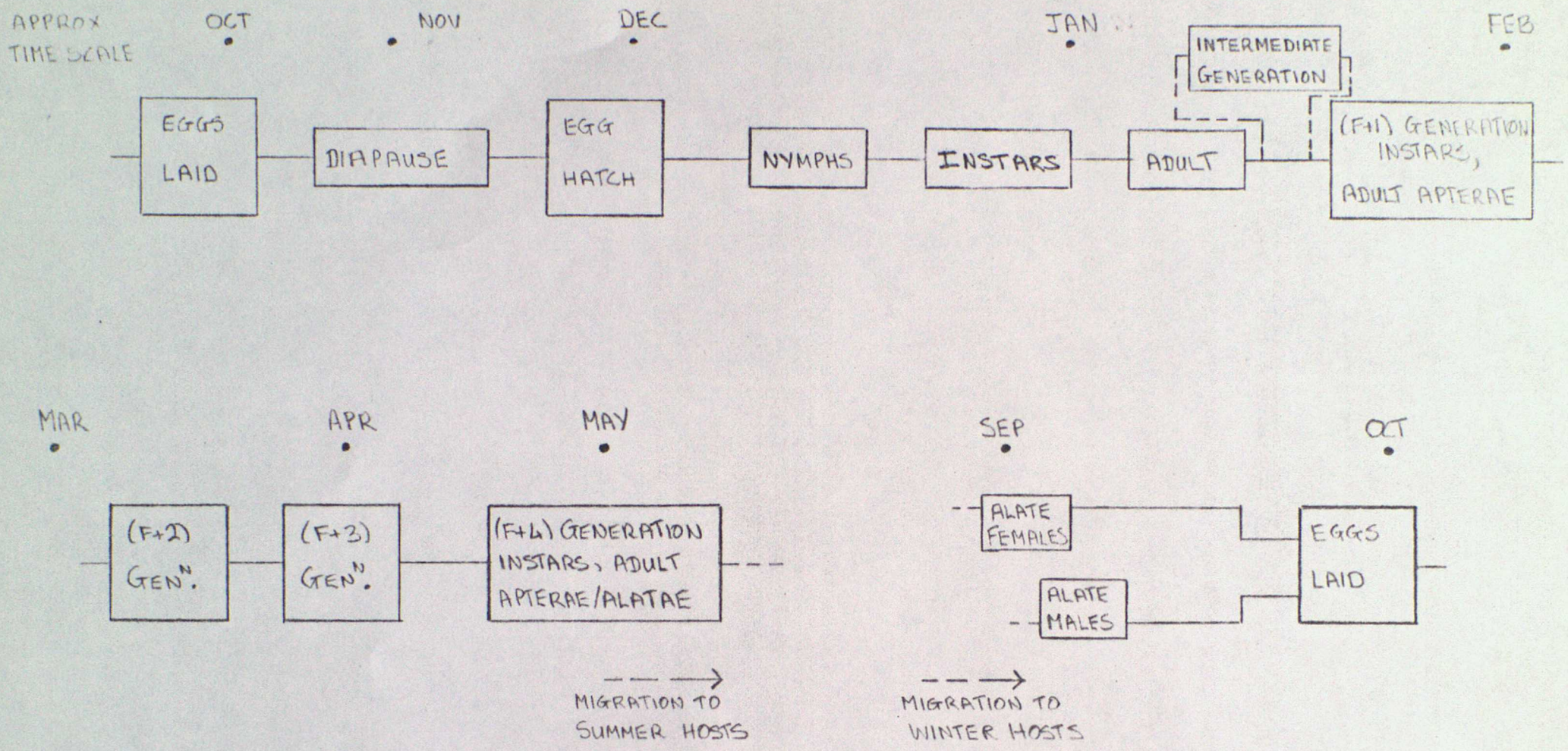
Table 4b

	SSM
Observed STD DEVN	543.6
RMS difference of (Observed-Calculated) using	
Calculated DOT	583.2
Actual DOT	453.8

Table 5

YEAR	OBSERVED			CALCULATED			
						SSM	
	DOFF	DOT	SSM	DOFF	DOT	Using Calc DOT	Using Obs DOT
1974	136	138	2453	119.3	138.5	1012.3	1039.4
1981	113	139	289	-	-	910.6	985.8
1982	117	138	143	108.1	133.6	1311.8	1039.4

Comparison of observed and calculated parameters on occasions not used in the derivation of the regression equations.



APPROXIMATE LIFE CYCLE OF BRACHYCAUDUS HELICHRYSI

FIG 1a

Fig 1b

WEEKLY TRAP CATCHES AT LONG ASHTON (1979)

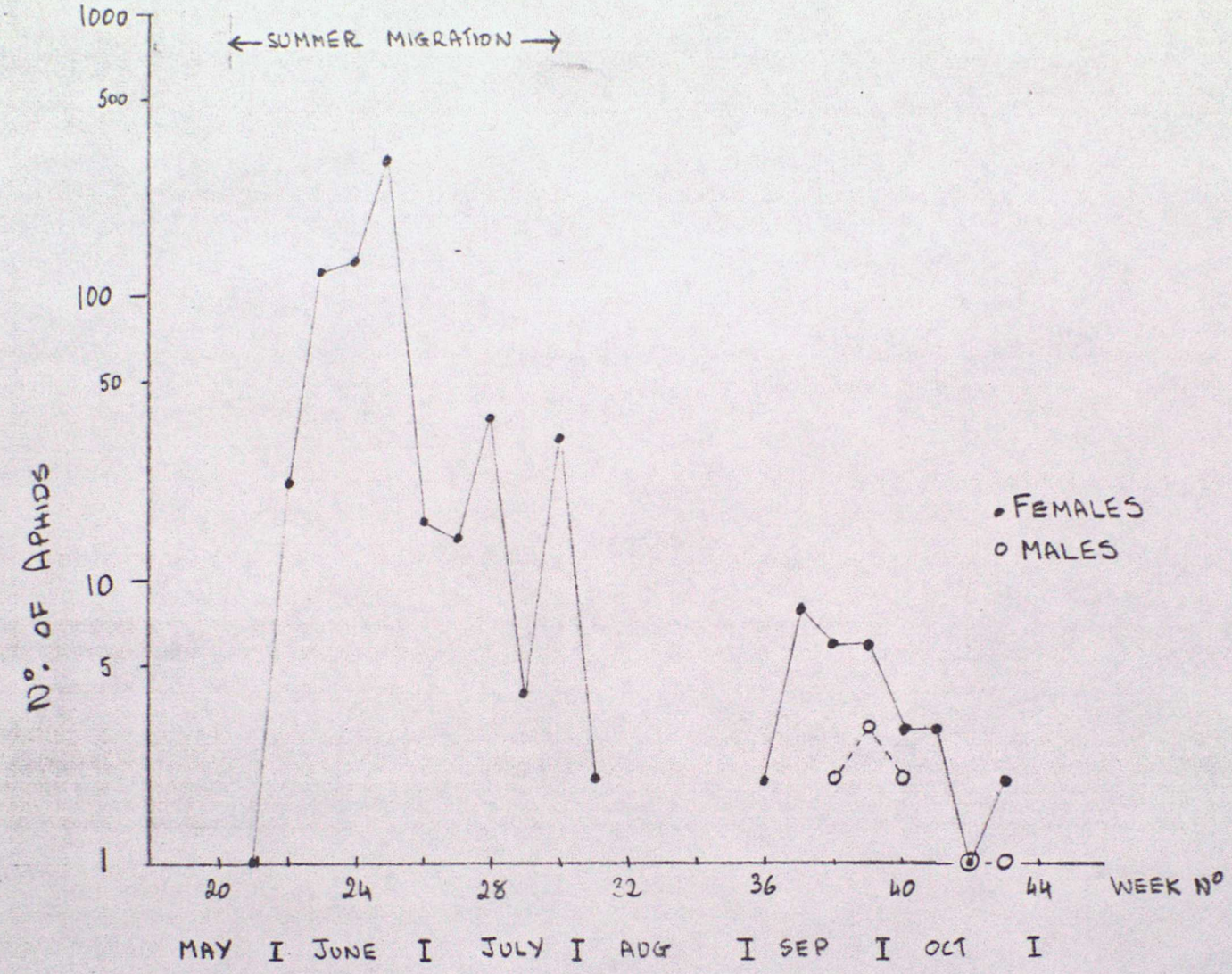


FIG 2

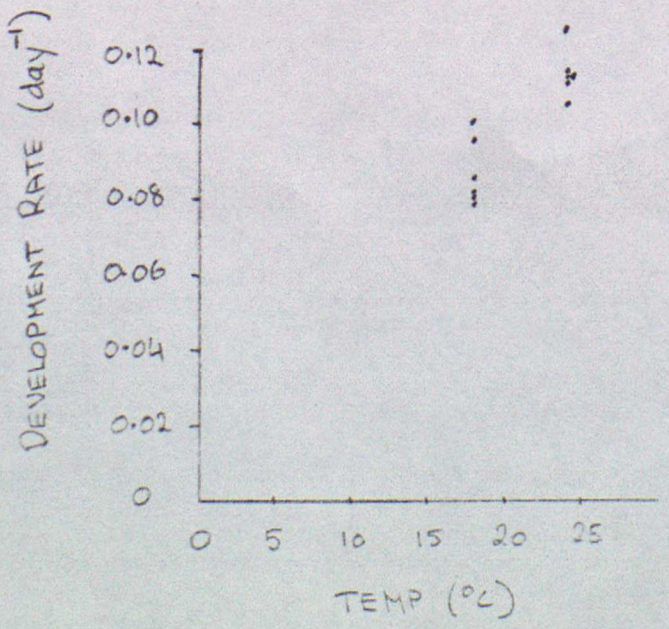
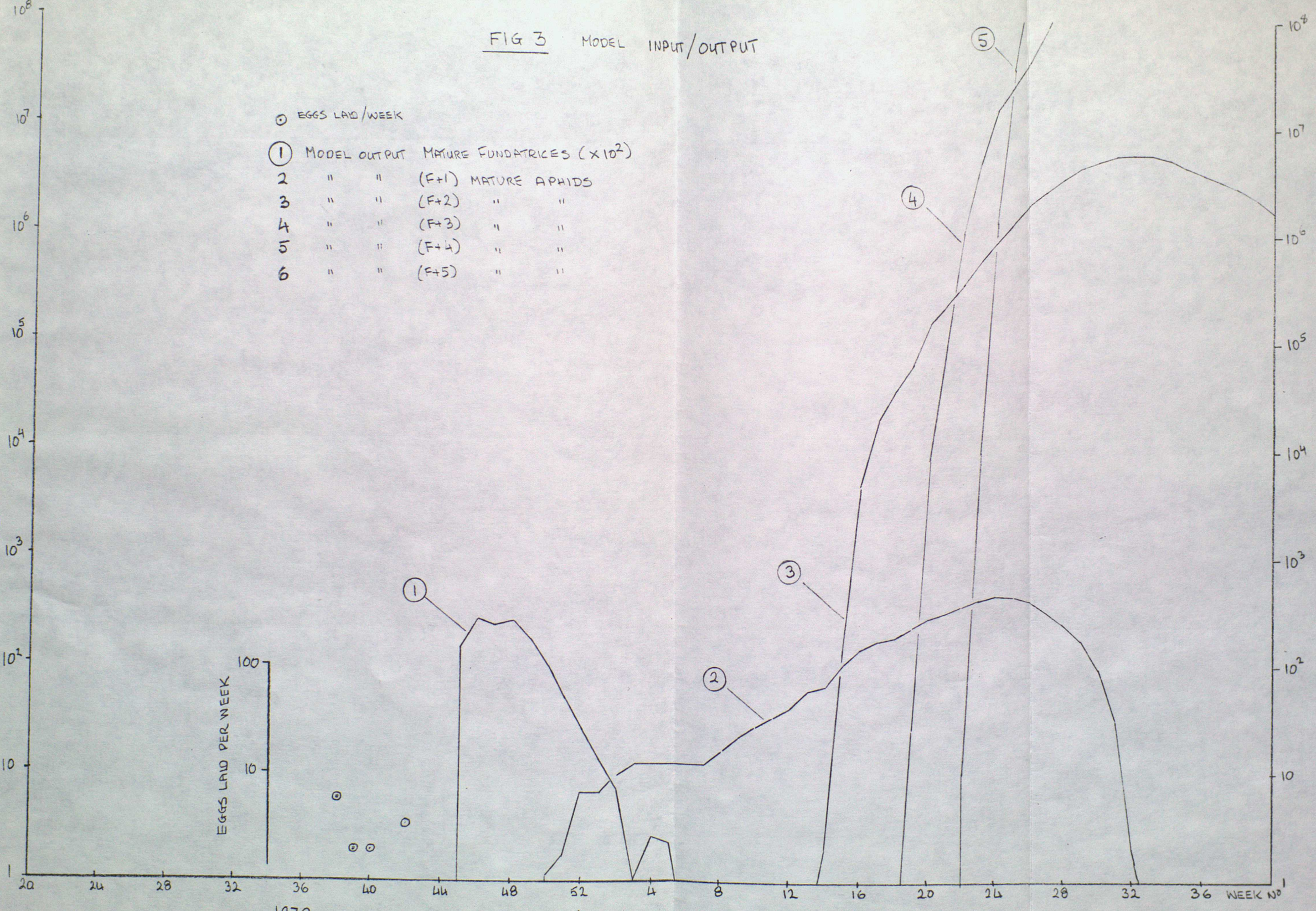


FIG 3 MODEL INPUT/OUTPUT

⊙ EGGS LAID/WEEK

(1) MODEL OUTPUT MATURE FUNDATRICES ($\times 10^2$)
2 " " (F+1) MATURE APHIDS
3 " " (F+2) " "
4 " " (F+3) " "
5 " " (F+4) " "
6 " " (F+5) " "



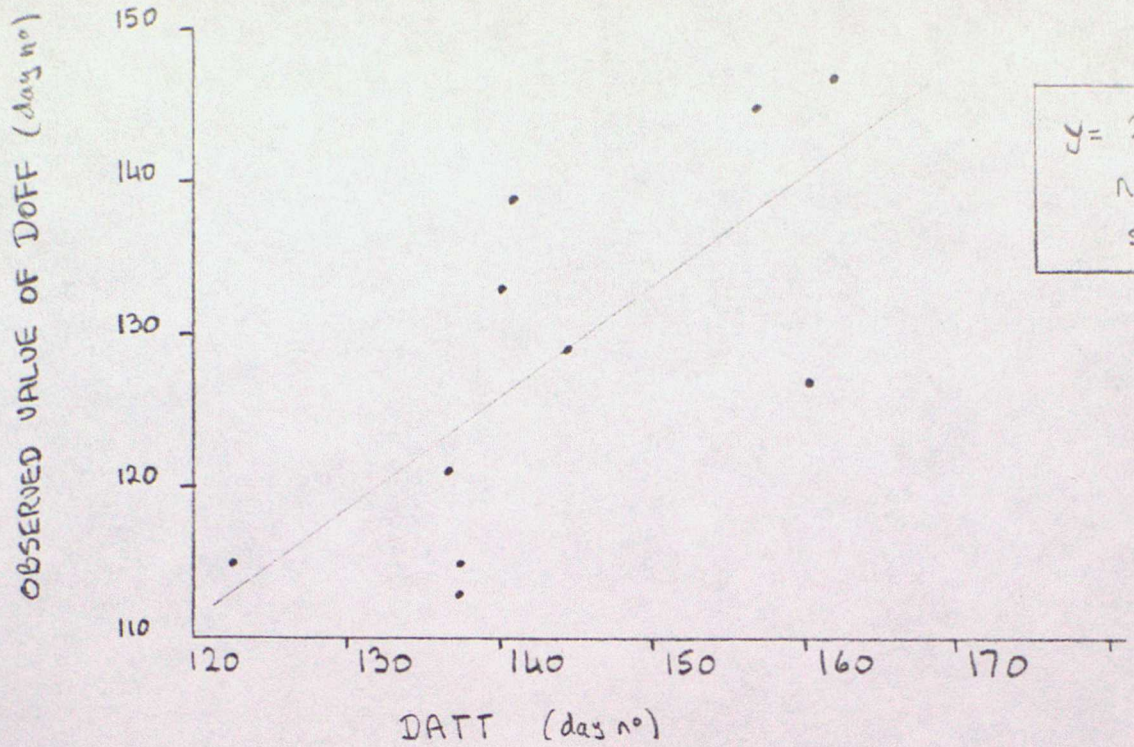

OBSERVED VALUE OF DOFF (day nº)
150
140
130
120
110
120
130
140
150
160
170
DATT (day nº)
y = 23·73 + 0·73x
n = 10, r = 0·70
sig ~ 2%

FIG 4a

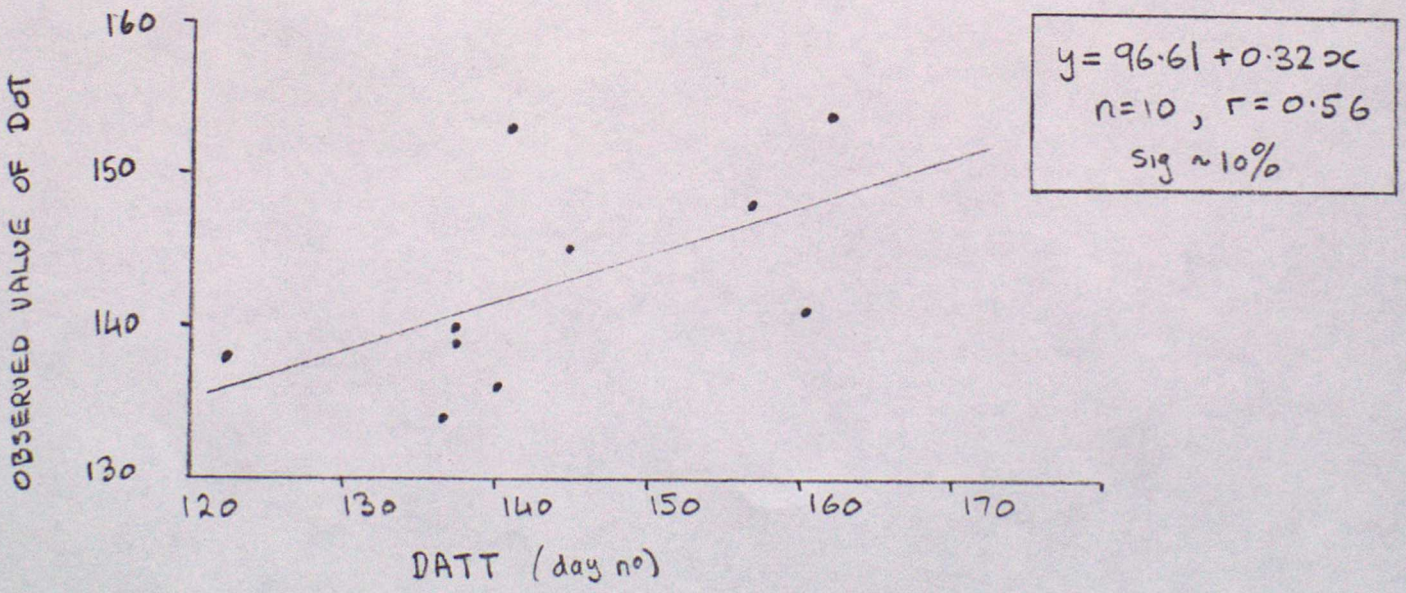

OBSERVED VALUE OF DOT
160
150
140
130
120
130
140
150
160
170
DATT (day nº)
y = 96·61 + 0·32x
n = 10, r = 0·56
sig ~ 10%

FIG 4b

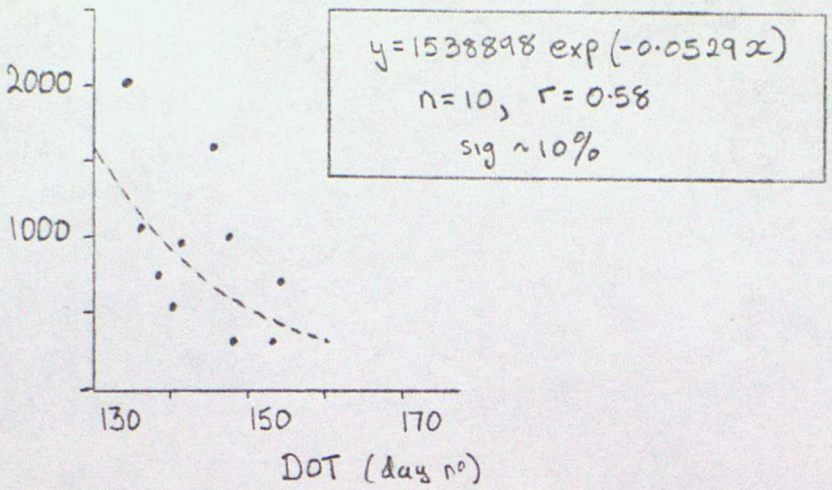

y=1538898 exp(-0.0529x)
n=10, r=0.58
sig ~10%
2000
1000
130
150
170
DOT (day n°)

FIG 5

Fig 6a

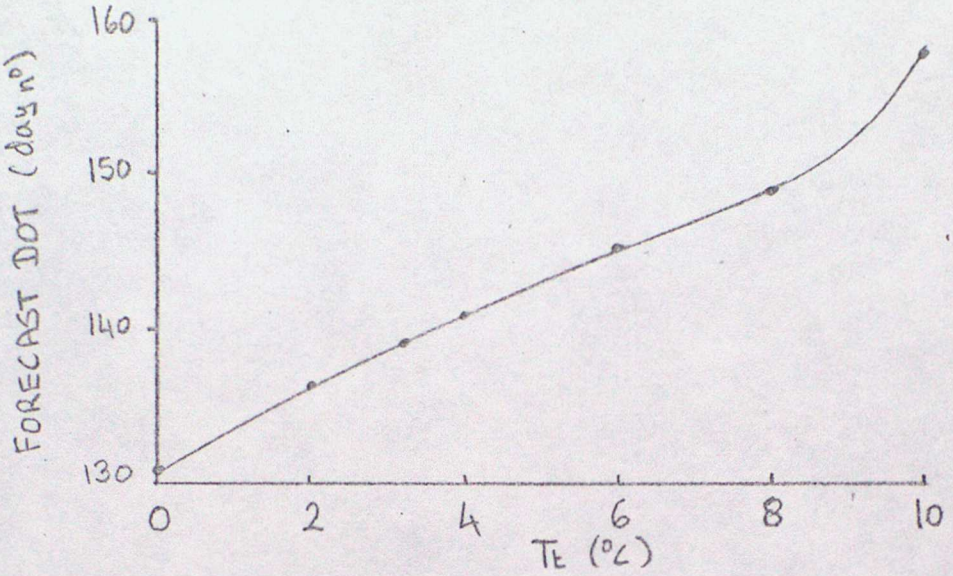
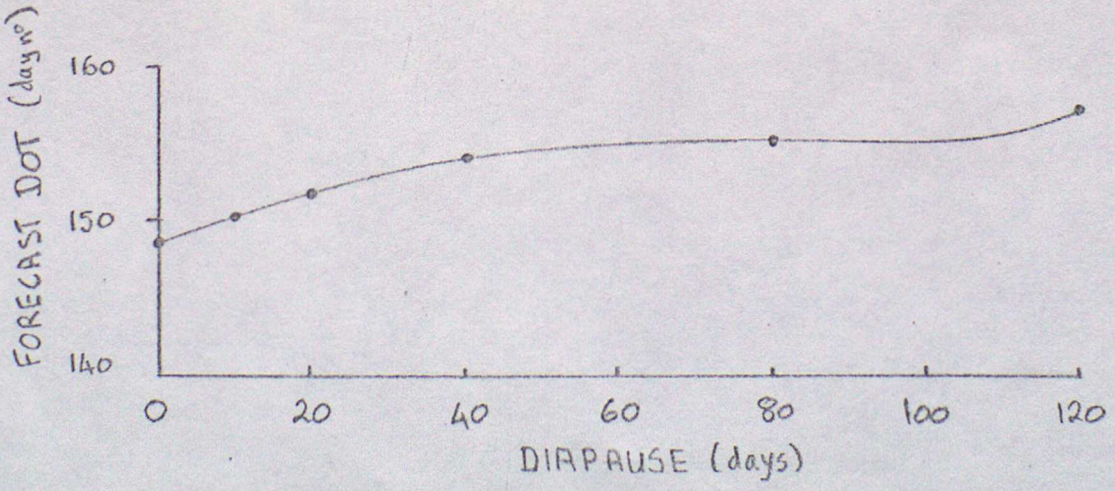

FORECAST DOT (day n°)
160
150
140
130
0
2
4
6
8
10
TE (°C)

Fig 6b


FORECAST DOT (day n°)
160
150
140
0
20
40
60
80
100
120
DIAPAUSE (days)

160
150
140
130
FORECAST DOT (day n°)
200
210
220
230
240
START OF EGG LAYING (day n°)

Fig 6c

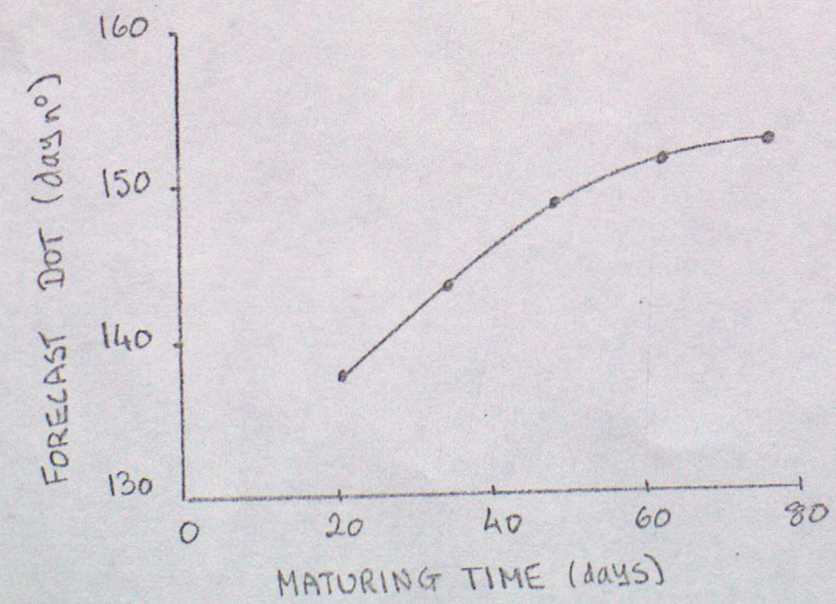

160
150
140
130
FORECAST DOT (day n°)
0
20
40
60
80
MATURING TIME (days)

Fig 6d

CORRELATION OF SSM AND T_{MIN}

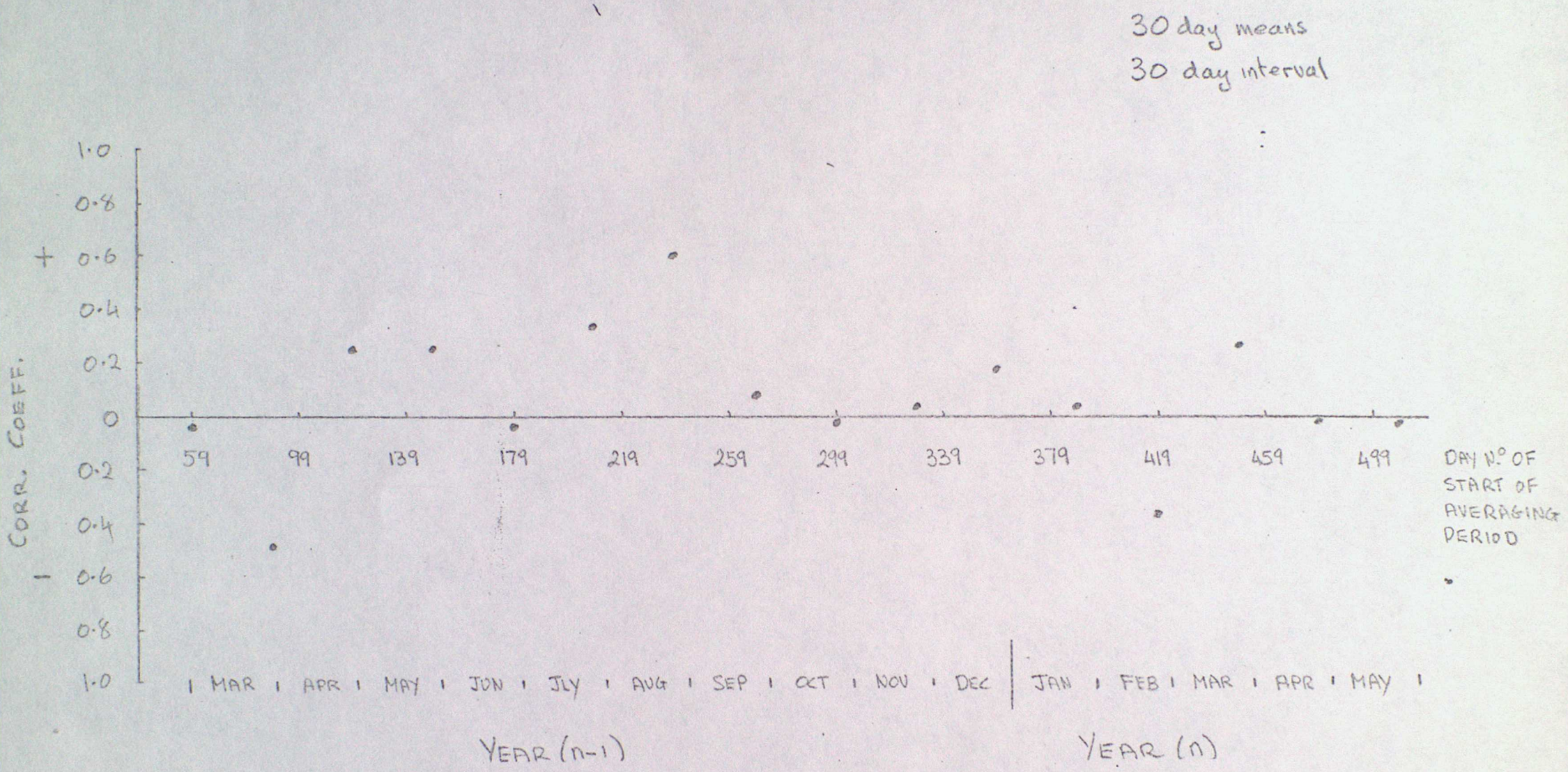


FIG 7

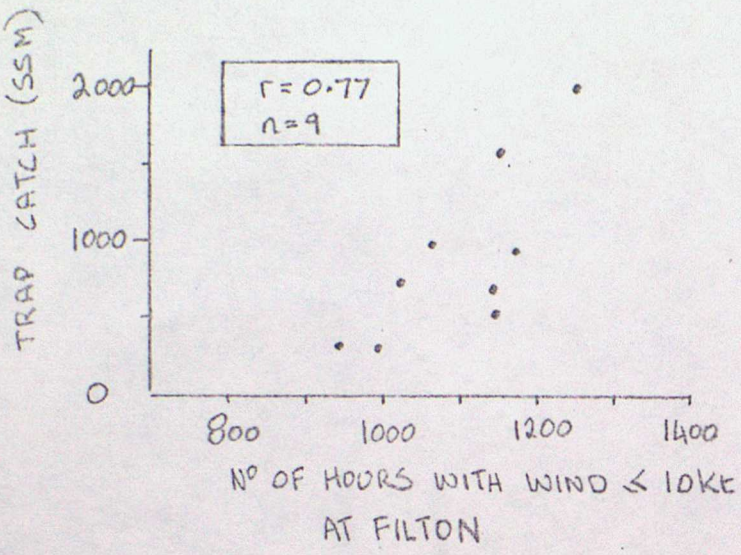


FIG 8 a

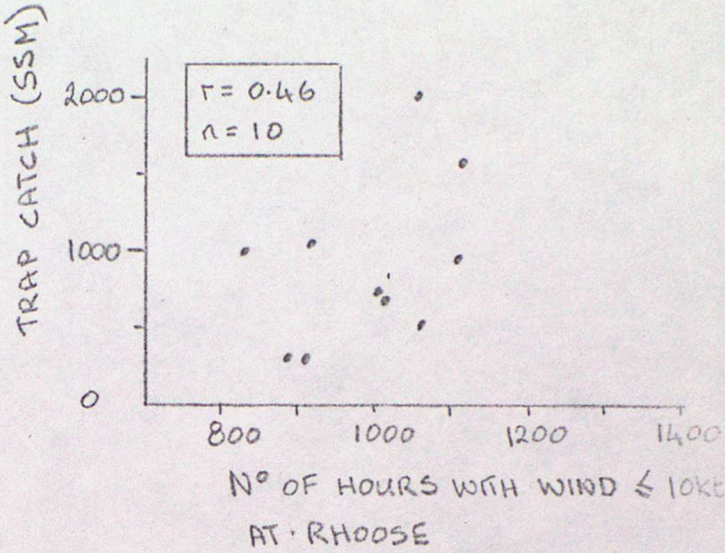


FIG 8 b

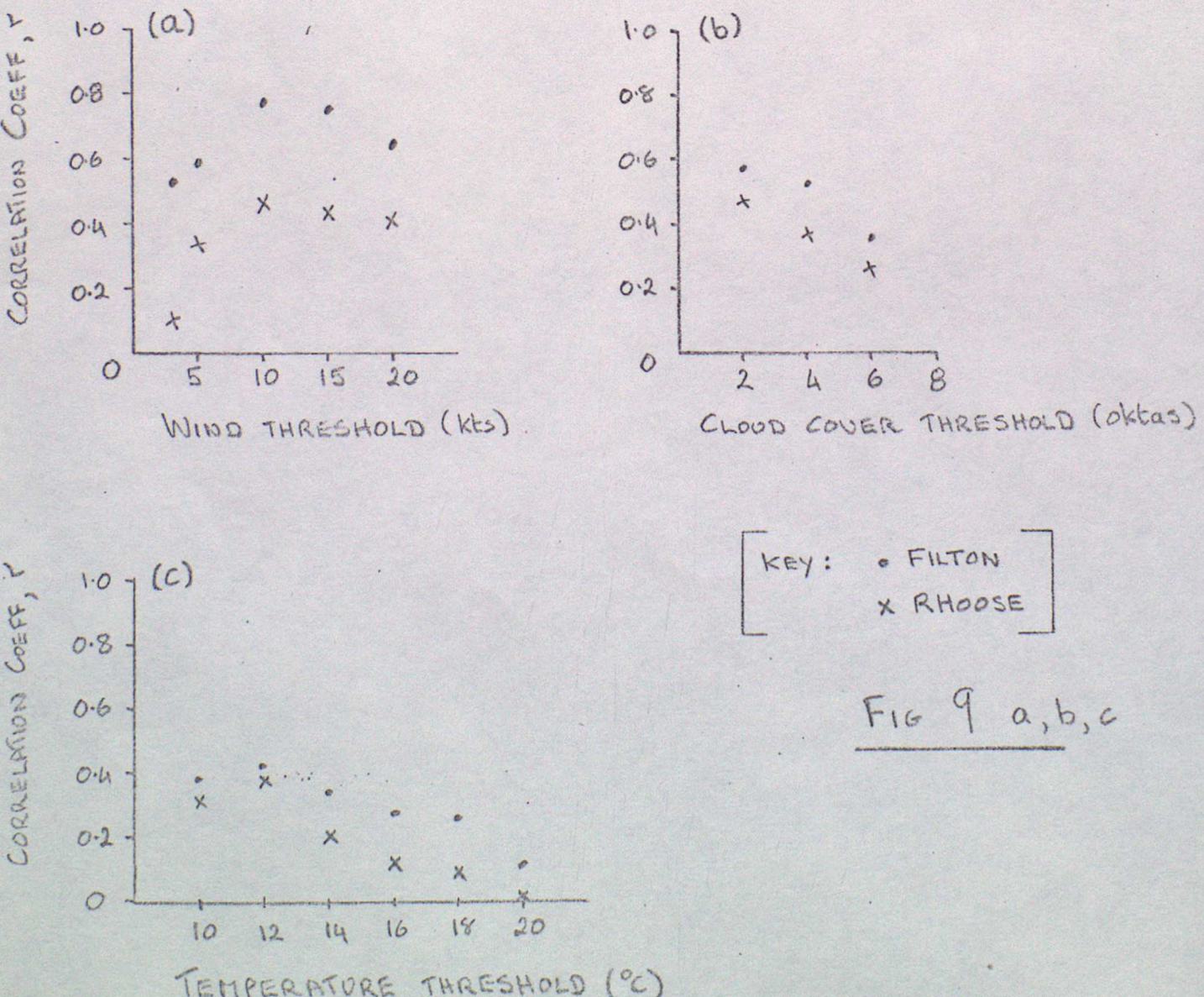


FIG 9 a, b, c